

Morphological Plasticity in the Tropical Sponge *Anthosigmella varians*: Responses to Predators and Wave Energy

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Abstract. The goal of the research presented here was to examine phenotypic plasticity exhibited by three morphotypes of the common Caribbean sponge *Anthosigmella varians* (Duchassaing & Michelotti). We were interested in examining the biotic (and, to a lesser extent, abiotic) factors responsible for branch production in this species. We also tested the hypothesis that the skeleton may serve an anti-predator function in this sponge, focusing on vertebrate fish predators (*i.e.*, angelfish) in this work. In transplant and caging experiments, unprotected forma *varians* replicates were immediately consumed by angelfish, while caged replicates persisted on the reef for several months. These findings support the hypothesis that predators (and not wave energy) restrict forma *varians* to lagoonal habitats. Branch production was not observed in *A. varians* forma *incrustans* when sponges were protected from predators or placed in predator-free, low-wave-energy environments. It is not clear from our work whether forma *incrustans* is capable of producing branches (*i.e.*, whether branch production is a plastic trait in this morph). Additional field experiments demonstrated that *A. varians* forma *varians* increased spicule concentrations, compared to uninjured sponges, in response to artificial predation events, and *A. varians* forma *rigida* reduced spicule concentrations, compared to uncaged controls, when protected from predators. These findings indicate that spicule concentration is a plastic morphological trait that can be induced by damage, and that *A. varians* may be able to reduce spicule concentrations when environmental conditions change (*e.g.*, in the absence of predators). The potential significance of inducible defenses and

structural anti-predator defenses in sponges is discussed in relation to recent work on sponge chemical defenses.

Introduction

Morphological antipredator defenses, whether constitutive or induced, are common and effective strategies for marine organisms with hard body coverings (Harvell, 1984; Lively, 1986; Vermeij, 1987; Trussell, 1996). For soft-bodied marine organisms (*e.g.*, seaweeds and many invertebrates), morphological options to defend against predation are typically limited. Because of this, marine ecologists have focused attention over the past two decades on chemical defensive strategies adopted by organisms that appear physically vulnerable to attack. For example, our understanding of general principles of chemical ecology has increased greatly because of detailed work done with seaweed chemical defenses (*e.g.*, Fenical, 1982, 1997; Faulkner, 1984, 1998; Hay and Fenical, 1988; Schnitzler *et al.*, 2001).

Chemical ecologists have successfully extended this work to marine invertebrates, and studies have demonstrated the defensive importance of secondary metabolites in several invertebrate taxa (*e.g.*, Bakus, 1981; Coll and Samarco, 1988; Duffy and Paul, 1992; Paul, 1992; Pawlik *et al.*, 1995). Much of this work has focused on coral reefs, where predation rates are typically high (Bakus, 1964, 1966; Huston, 1985). Among coral reef invertebrates, sponges have received a great deal of recent attention because these common soft-bodied organisms have impressive capabilities for producing secondary metabolites (see review in Pawlik, 1997). It seems clear that chemical defenses in sponges have been an extremely common and successful evolutionary strategy for dealing with high rates of predation found on coral reefs. For instance, Pawlik *et al.* (1995)

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found that out of 71 species examined, 44 sponges had deterrent effects on the non-spongivorous fish *Thalassoma bifasciatum*. Although the focus has been on vertebrate predators, invertebrates are also important sponge predators (Guida, 1976; Pawlik, 1983), and Waddell and Pawlik (2000a, b) recently demonstrated that crude extracts from several species of Caribbean sponge deterred predation by two species of sea star and the hermit crab *Paguristes puniticeps*.

It should be noted that neither *T. bifasciatum* nor *P. puniticeps* is known to consume sponges in the wild (Pawlik *et al.*, 1995; Waddell and Pawlik, 2000a). Determining whether chemicals have deterrent properties is technically difficult, but it is clear that tests should be performed with organisms that consume sponges, because chemical defenses are not equally effective against all consumers (*e.g.*, Pennings *et al.*, 1994; Cronin *et al.*, 1997; Ridenhour *et al.*, 1999). For example, the specialized fish predator *Chaetodon melannotus* feeds on octocorals that can produce highly toxic compounds (Alino *et al.*, 1992). Indeed, *C. melannotus* uses the "toxic" compounds produced by its octocoral prey as a cue when locating prey (Alino *et al.*, 1992). In feeding assays, these compounds would probably be avoided by generalist predators like *T. bifasciatum*, thus providing misleading ecological information about chemical defense in octocorals if results are extrapolated to all potential predators. Whether the most conspicuous and abundant spongivores—primarily angelfish (Randall and Hartman, 1968; Hourigan *et al.*, 1989; Wulff, 1994; Hill, 1998)—are affected by crude extracts from sponges remains an important unanswered question.

In their classic study of spongivorous fish, Randall and Hartman (1968) proposed that sponges use spicules, noxious chemicals, and tough fibrous components in defense against predation. Despite the sharp, needlelike structure of many spicules and the relative indigestibility of spongin, these two traits have recently been described as serving little or no antipredator function in Caribbean sponges (Pawlik *et al.*, 1995; Chanas and Pawlik, 1995, 1996; Waddell and Pawlik, 2000a, b). The data supporting these claims are based on several feeding assays in which consumers are presented with spicules or slices of freeze-dried skeleton embedded in a squid-carrageenan matrix (*e.g.*, Chanas and Pawlik, 1996). However, much of the defensive functionality of the skeleton may be destroyed when spicules lose their natural orientation, or when strips of skeleton are disconnected from the supporting skeletal matrix.

Although Pawlik and colleagues have dismissed any antipredator role for the sponge skeleton (Chanas and Pawlik, 1996; Waddell and Pawlik, 2000a, b), structural components have been shown to serve defensive roles in other soft-bodied reef invertebrates capable of chemical defense (*e.g.*, Harvell and Fenical, 1989). West (1997, 1998) showed that sclerite production was induced in response to

simulated predator damage in the common gorgonian coral *Briareum asbestinum*. Furthermore, *B. asbestinum* is able to modulate spicule morphology depending on the context or position of simulated attacks (West, 1997). It is not clear whether a similar situation exists in sponges. However, several testable predictions follow from the hypothesis that skeletal structures serve defensive purposes in sponges. Common reef sponges that are chemically undefended (*e.g.*, *Anthosigmella varians*, *Mycale laevis*, and *Niphates erecta* [Pawlik *et al.*, 1995]) and experience low rates of predation would be predicted to have skeletal structures that deter spongivores. Although Chanas and Pawlik (1995, 1996) found that the skeleton of some sponges was not a deterrent to *T. bifasciatum*, optimally foraging spongivores may have a different response. Another prediction (based on the assumption that the modification or elaboration of skeletal structures is an energetically expensive process (*e.g.*, Palumbi, 1984, 1986)) is that a positive correlation should exist between sponge spicule or spongin concentrations, and predator presence or attack frequency. In this study, we tested the prediction that skeletal structures respond plastically to predation in the tropical sponge *Anthosigmella varians* (Duchassaing & Michelotti), focusing on the effects of angelfish, a major group of spongivores (Randall and Hartman, 1968).

Furthermore, we examined some of the factors responsible for branch production in *A. varians*. *Anthosigmella varians* is a common sponge that exhibits discontinuous morphological variation on Caribbean reefs (Fig. 1; see also Wiedenmayer, 1977; Vicente, 1978; Hill, 1999). Many of the major distinguishing morphological characteristics are detailed in Table 1. Wiedenmayer (1977) separated the encrusting morph (*A. varians* forma *incrustans*) from the amorphous, irregularly lobate, branching form (*A. varians* forma *varians*). Forma *incrustans* is conspicuous on fore- and back-reefs and can cover large areas of reef substrate (Table 1; Vicente, 1978; Hill, 1999). Forma *varians* is typically found in shallow, lagoonal areas; it covers smaller patches of substrate, but some branches can extend up to 40 cm into the water column. Hill (1999) reported a third morph (*A. varians* forma *rigida*) that produced forma *variens*-like branches but had a stiff skeletal construction. Forma *rigida* and forma *incrustans* occur sympatrically on shallow reefs, whereas forma *variens* is found only in areas without predators (Table 1). Hill (1999) proposed that the thick cortex found in forma *rigida* was a response to, and defense against, sponge predators. Vicente (1978) hypothesized that forma *variens* was restricted to shallow, lagoonal environments because it is incapable of tolerating habitats with high wave energy. In previous work with *A. varians*, we found that sponges with spongin-fortified skeletons coexisted with predators, but sponges with low levels of spongin were restricted to predator-free habitats (Hill, 1999).

We had two major goals with the research reported here. The first was to test whether the *A. varians* skeleton responds to predation in the direction predicted if structural components serve a defensive function. The second goal was to test Vicente's (1978) hypothesis that *A. varians*

forma varians is restricted to low-wave-energy environments (e.g., lagoons, bays) because their branches would be destroyed on the open reef.

Materials and Methods

Predator exclusion and wave energy

Using a combination of transplantation and caging, *Anthosigmella varians* *forma varians* individuals were placed on Alligator reef in the Florida Keys (24°51'N; 80°37'W) at a depth of 10 m. The first aim of this experiment was to determine whether *forma varians* could exist in branching form in the presence of spongivores. The second aim was to test Vicente's (1978) hypothesis that *forma varians* is unable to persist on the open reef in an environment with relatively high wave energy. The Alligator site was chosen because it has substantial angelfish populations, and because it faces the open ocean, thus experiencing greater water motion (waves and currents) than the Florida Bay.

We cut 5-cm-long branches from 40 different sponges growing in waters adjacent to Long Key (24°50'N; 80°49'W). We made every effort to collect sponges that were separated from one another by at least 15 m to minimize the possibility of collecting genetically identical individuals. These explants were attached, upright, to 8 × 8 × 0.5 cm CaCO₃ blocks with monofilament, and were grown for about 90 days in Buttonwood Sound at a depth of 1 m near the Key Largo Marine Research Laboratory (KLMRL), Key Largo, Florida. Once sponges had covered a large portion of the block (≈75% of available surface area) and demonstrated signs of boring (calcareous chips on the sponge surface), we placed the 40 blocks on the reef in an area frequented by spongivores. A suite of predators consume sponges, but the major vertebrate spongivores on Caribbean reefs are angelfish (Randall and Hartman, 1968; Hourigan *et al.*, 1989; Wulff, 1994). Blue, queen, gray, and french angelfish were observed at the Alligator site (Hill 1999), and our experiments were located within a gray angelfish territory.

Blocks were attached with flagging tape to wooden planks anchored to the substratum, and cages ($n = 20$) were placed over half of the blocks. The other 20 replicates were exposed to predators. Exclosures were made of plastic caging material (Vexar) with a mesh size of 5 cm (see Fig. 2).



Figure 1. *Anthosigmella varians*. (Top) *A. varians* *forma incrustans* is located on Caribbean fore reefs. It assumes an encrusting morphology and bores into calcium carbonate structures. This individual is growing over a colony of *Montastrea cavernosa*, and the debris on the surface of the sponge is evidence of boring. (Middle) *A. varians* *forma varians* is found in shallow, lagoonal habitats. It produces sinuous branches that can exceed 40 cm in height. (Bottom) *A. varians* *forma rigida* produces *forma varians*-like branches from a mounding base and has a thick cortex that produces a rigid skeleton. It is sympatric with *forma incrustans*.

Table 1

Some major morphological and ecological differences observed among the three *Anthosigmella* varians morphotypes in the Florida Keys

Character	forma <i>incrustans</i>	forma <i>varians</i>	forma <i>rigida</i>
Distribution of sponges	Reef	Bay/near island	Shallow reef
Depth (m)	8–27	1–3	8–13
Branches	Absent	Present	Present
Branch length (cm)	n/a	10	4
Area of attachment (cm ²)	1430	68	36
Tissue strength (N)	5	2	>10
Cortex thickness (mm)	1	Absent	6
Spicule concentration (mg cm ⁻³)	52	112	168
Subtylostyle length (μm)	355	375	375
Subtylostyle width (μm)	8	12	8
<i>Anthosigma</i> shape	Single bend	Two or more bends	Single bend

Values represent approximate averages (modified from Hill (1999)). Predators are found on the reef (in forma *incrustans* and forma *rigida* habitats), but are rare or absent in the nearshore environments or in Florida Bay (i.e., in forma *varians* habitats).

The effects of predators were obvious within the first week, but the experiment ran for 125 days to determine whether any of the transplanted sponges adopted an encrusting morphology. At the conclusion of 125 days, changes in branch height were measured and compared using a one-tailed *t* test (Zar, 1984).

Given that *A. varians* forma *rigida* populations were sparse, we conducted a predator exclusion study on only 10 individuals from this morphotype. Those individuals were collected from Alligator and Tennessee (24°44'N; 80°47'W) reefs, and we made every effort to collect genetically distinct sponges by sampling sponges separated by more than 10 m. These sponges were affixed to ceramic tiles (15 cm × 15 cm) by monofilament. The experiment was run on Tennessee reef at a depth of 8 m, and a number of angelfish were observed at this site (Hill, 1998). As with the Alligator site, this site is exposed to open-ocean water motion. Five replicates were caged, the other five were exposed to predators. After 11 months, changes in spicule concentrations were compared. We measured spicule concentrations by excising a piece of sponge and measuring dimensions so that we could determine volumes. Thus, all spicule densities were standardized to a known sponge volume. Spicules were cleaned of sponge material with nitric acid and washed with double distilled H₂O. We measured spicule mass after drying spicules at 60°C for 48 h, and compared average spicule concentrations (milligrams of spicule per cubic centimeter of sponge) between treatments using a one-tailed *t* test (Zar, 1984). The *a priori* reason for predicting that spicule concentration would decrease (and hence our use of one-tailed *t* tests) was based on work by Palumbi (1986) showing that lower spicule densities were correlated with weaker sponge tissue.

To determine the influence of predators on branch production in *A. varians* forma *incrustans*, we placed exclo-

tures made of plastic caging material (Vexar) with a mesh size of 5 cm over 13 individuals at a depth of 18 m on Tennessee reef. Cages were attached to the substratum using masonry nails and plastic cable ties. In some cases the cage did not cover the entire sponge (Fig. 2b). Nine additional, topless cages (which allowed predator access to the sponge) were placed over sponges to serve as controls for any cage artifacts. Sponges were monitored for about 450 days for production of branches, and cages were cleaned of fouling algae with a frequency of every month or less. We tested for differences in water flow between treatments by measuring the rate of dissolution of plaster-of-paris clods (Wellington, 1982). To achieve equal sample sizes in our statistical tests, we deployed clods within all 9 of the topless cages and within 9 of the 13 predator exclusions. Clods were removed after 2 d. To assess the effect of lower wave energy on morphology, 8 forma *incrustans* individuals were transplanted to Florida Bay at a depth of 1 m (adjacent to the KLMRL). Samples (≈100 cm²) were collected with a hammer and chisel from sponges on Tennessee reef. Specimens were attached to cinder blocks with monofilament within 4 h, and transplants were monitored for more than 8 months for the production of branches.

Artificial predation

We conducted an artificial predation experiment to see if this would cause forma *varians* to increase spicule concentration during simulated predation events. Using the protocol described in the section on forma *varians* above, 60 branches (≈4–5 cm in height) were collected from different forma *varians* sponges near Long Key, and attached to calcareous blocks. The experiment was conducted at 1-m depth in Buttonwood Sound. Thirty sponges were clipped with a pair of scissors each day for 43 days to

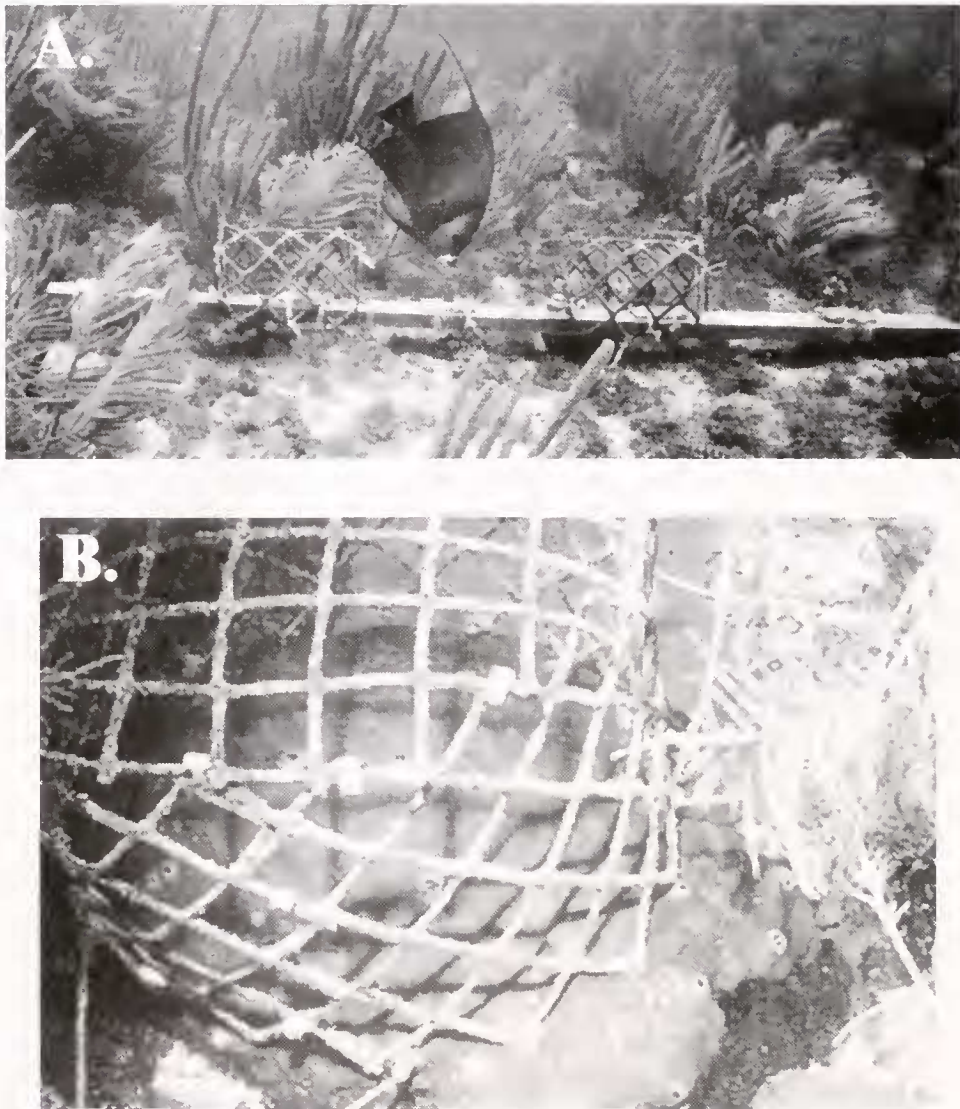


Figure 2. Experimental setups in the field. The material used to create these enclosures (Vexar) was used in all caging experiments. (A) The gray angelfish shown in this picture immediately began to consume exposed sponges after replicates were placed on the reef, and almost all pretransplant height was lost in the first week. The gray angelfish was one of a pair that had a territory in this area. Other angelfish (french, blue, and queen) and a Hawksbill turtle were seen in this area during the experiment. (B) An enclosure placed over a particularly large *forma incrustans* individual. Cages were effective at keeping predators out, but in replicates where the cage did not cover the entire sponge, fish could still bite exposed parts of the sponge (see marks outside of cage on lower right).

simulate wounds from a feeding event: another 30 sponges were left uninjured. Random regions along the length of the sponge branch were clipped each day, and different regions were injured between clippings. Although our simulated predation events differed qualitatively from natural angelfish bites, our objective was to determine whether *A. varians* was capable of modifying spicule concentrations after injury. At the end of the experiment, the entire branch from each replicate was frozen and transported to the laboratory for spicule analysis. For spicule concentration

measurements, sections of known volume were taken from areas that appeared to have been injured for replicates in the artificial predation treatment, and from randomly chosen areas in the control replicates. Averages were compared as described above. The *a priori* reason for predicting increased spicule concentrations in the artificial predation treatment (and hence our use of one-tailed *t* tests) was based on work by Palumbi (1986) showing that spicule density and tissue stiffness and strength were positively correlated.

Results

Predator exclusion and wave energy

Transplanting *Anthosigmella varians* forma *varians* onto the reef produced dramatic results. A suite of spongivores was attracted to transplanted forma *varians*, and uncaged replicates were consumed rapidly (attacks began within 5 min; Fig. 2a). Angelfish removed virtually all above-substratum sponge tissue within the first week. Even though predators were quickly identified as a powerful selective force, we were interested in determining whether transplanted forma *varians* would adopt the morphology typical of forma *incrustans*. They did not, and some sponges ($n = 4$) increased height (*i.e.*, put energy into upward growth as opposed to encrustation) during the experiment. After several visits during the first week of the experiment, we visited the site about every 30 days to clean cages and monitor growth. This included visits before and after the passage of Tropical Storm Gordon (1994). The storm was responsible for the loss of one experimental unit containing several replicates (our buoy was attached to this structure), but appeared to have no effect on the replicates that remained (Fig. 3a). Other replicates were lost when the flagging tape failed to hold blocks to the wooden panels (these losses were not caused by the storm). At the end of this experiment, survivorship was high in the caged treatment, but was less than half in the uncaged treatment (Fig. 3b). Individuals exposed to predators (*i.e.*, uncaged) lost all pretransplantation height (largely within the first week of the experiment), and this was significantly different from the caged treatment ($t = 7.98$, d.f. = 14, $P \leq 0.001$). As can be seen in Figure 3b, the only survivors from the uncaged treatment were found within calcareous blocks (*A. varians* is a bioeroder).

Forma *rigida* had significantly lower spicule concentrations in the predator-exclusion treatment compared to the uncaged control ($t = 1.96$; d.f. = 8, $P < 0.05$; Fig. 4). Individuals from the uncaged control had spicule concentrations that were statistically indistinguishable from those at the beginning of the experiment (Hill, 1999). Furthermore, we noticed gross morphological changes (*e.g.*, adoption of an encrusting morph and a spongier texture) in replicates from the caged treatment.

Two cages in the experiment involving forma *incrustans* could not be located midway through the experiment, but none of the 11 remaining caged forma *incrustans* individuals produced branches over the 450 days of monitoring. Judging from the dissolution of plaster-of-paris clods, enclosures apparently had no significant effect on water flow compared to uncaged controls ($t = 1.4$; d.f. = 16; $P > 0.15$). It was clear that spongivores were prevented from biting the caged portion of the sponge since evidence of predation was only observed on uncaged portions of the sponge (Fig. 2b). In addition, none of the 8 transplanted forma *incrustans* individuals produced branches when

placed in Florida Bay. Individuals transplanted into the bay lost zooxanthellar symbionts within 12 days, but recovered normal pigmentation when placed in the shade (Hill and Wilcox, 1998). This had no effect on survivorship since individuals persisted for another 8 months until a pulse of fresh water during the winter killed all replicates (W. Fitt, Key Largo Marine Research Laboratory, pers. comm.).

Artificial predation

During the artificial predation experiment involving forma *varians*, clipping resulted in significant increases in spicule concentrations compared to unmolested controls ($t = 2.14$; d.f. = 36; $P < 0.05$; Fig. 4). Injured areas were noticeably white (presumably because of increased spongin concentrations), and could be clearly demarcated from uninjured tissue. Twenty-two replicates were destroyed by snorkelers (10 from the unclipped treatment) and were not included in the analysis.

Discussion

The purpose of this research was to explore environmental factors that may be responsible for some of the observed morphological variability in *Anthosigmella varians*. Transplant and caging experiments involving forma *varians* demonstrated that this morph is highly vulnerable to fish predation (Fig. 2a). When the uncaged replicates were placed on the reef, angelfish immediately began consuming them, and the exposed sponges lost all of their pretransplant height within the first week of the experiment (Fig. 3). Pawlik (1998) also found that forma *varians* was consumed by a suite of spongivores when transplanted to the reef. Even in the presence of predators, however, forma *varians* was capable of surviving for several months by boring into limestone blocks, but these sponges suffered higher mortality than the replicates in the caged treatment (Fig. 3b). The fact that forma *varians* can persist in an unmodified form on the open reef when protected from predators refutes Vicente's (1978) hypothesis that wave energy is responsible for the discontinuous distribution of forma *incrustans* and forma *varians*. The transplanted sponges were exposed to tropical-storm-strength wave action, yet four of the caged replicates gained height during the course of the experiment, suggesting favorable environmental conditions for growth. This experiment, and Pawlik's (1998) data, indicates that predators, and not wave energy, are the primary selective agent restricting forma *varians* to shallow, lagoonal habitats.

Branch production was not observed in experiments with forma *incrustans*. Excluding predators *in situ* had no effect on morphology, nor did transplanting forma *incrustans* into Florida Bay. There are at least three explanations for the lack of phenotypic change observed in experiments involving this morphotype. First, encrustation may be a fixed (*i.e.*,

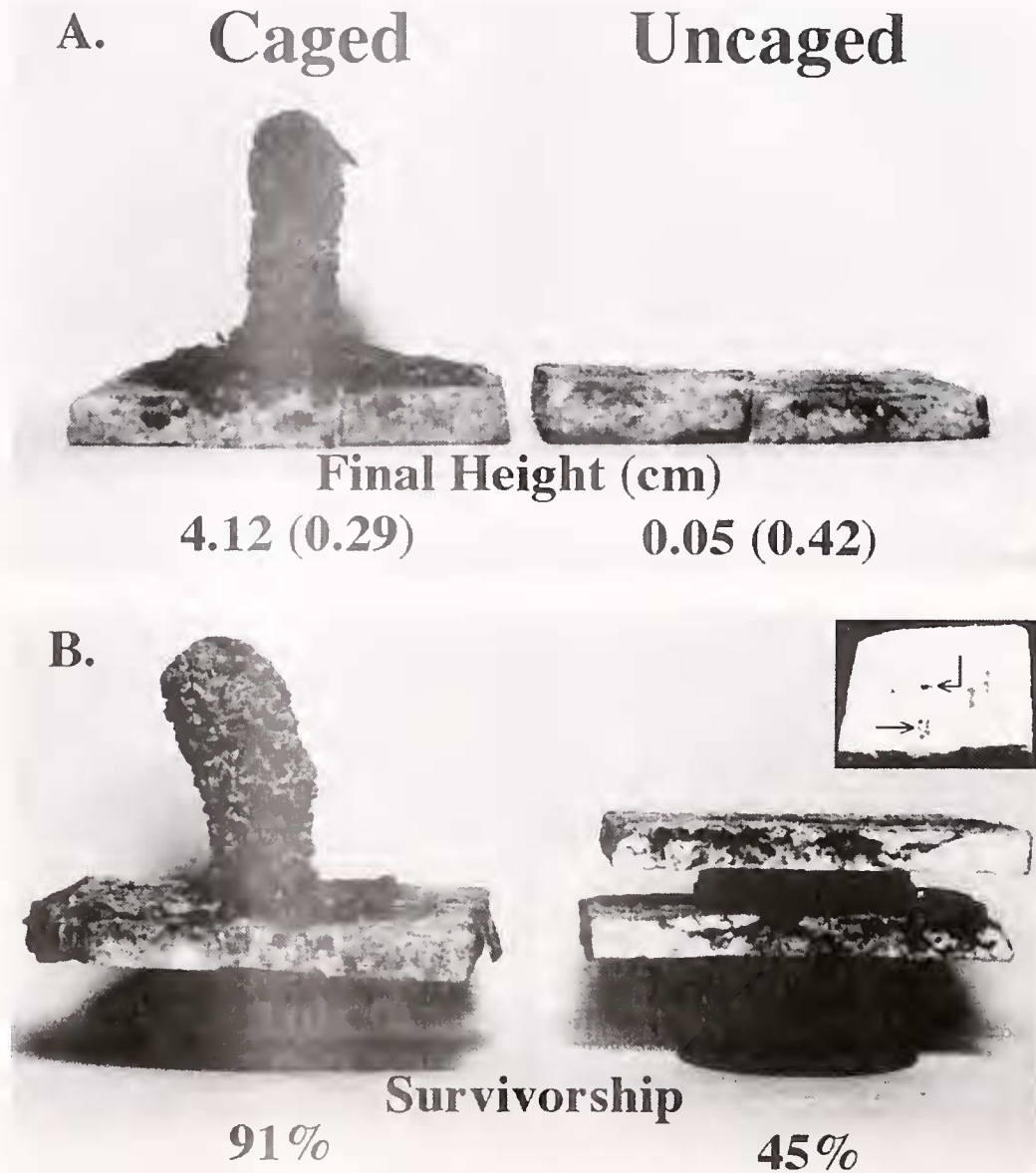


Figure 3. Data from transplant and caging experiments involving *Anthosigmella varians* forma *varians*. (A) Side view of caged (on left) and uncaged replicates. Average final heights (\pm SE) were significantly different ($t = 7.98$, d.f. = 14, $P < 0.001$) between caged ($n = 11$) and uncaged ($n = 5$) treatments. Uncaged replicates lost all of their pretransplant height, while two of the caged replicates gained in height over the course of the experiment. (B) Large differences in the survivorship of sponges from the two treatments were recorded. Although surviving caged sponges (left) were clearly visible, surviving sponges exposed to predation were visible only when the block they had attached to was broken open. Two halves of a block from an uncaged replicate (separated by a black plastic divider) are shown on the right. The inset shows the block before it was broken in half, and oscular openings can be seen on the surface (arrows). The spaces visible within the block on the right were created by boring activities of forma *varians*.

developmentally canalized) trait. Second, in many of the caged replicates, it was impossible to place exclosures over the entire sponge: thus, portions of the sponge were exposed to predators. There may be enough integration within an individual sponge to communicate predation in one part of the body to other parts of the sponge. Finally, it is possible

that not enough time had elapsed to allow phenotypic modulation. If encrustation is a response to a stressful environment (wave energy and predation intensity are both higher on the reef), then it is predicted that an organism will delay expression of a vulnerable trait, provided that it is plastic, long after the threat from a stress is gone (Palumbi, 1984;

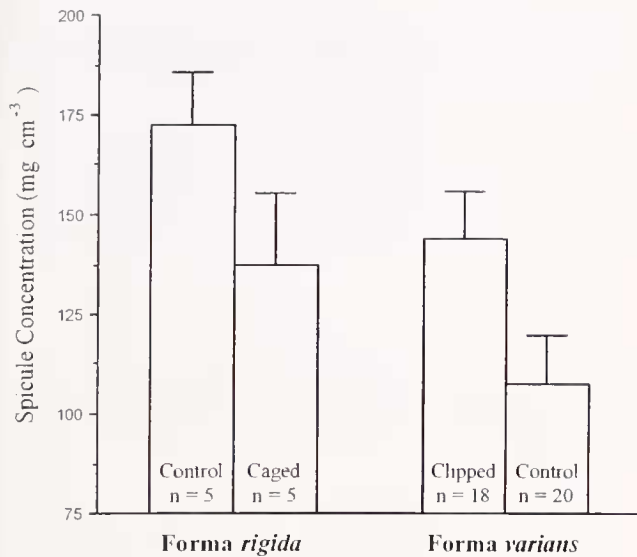


Figure 4. Average spicule concentration (\pm SE) as measured in experiments involving *Anthosigmella varians* forma *varians* and forma *rigida*. Sample sizes are shown in the figure. The bars on the left show results from the caging experiment involving forma *rigida*. Predator exclusion resulted in significant decreases in spicule concentrations compared to uncaged controls ($t = 1.96$; d.f. = 8, $P < 0.05$). The two bars on the right show the effects of artificial predation on spicule concentration in forma *varians*. Spicule concentrations increased significantly ($t = 2.14$; d.f. = 36; $P < 0.05$) in the clipped treatment compared to the unclipped control.

Sih, 1992). Longer periods of time might be necessary to observe branch production in forma *incrustans*. Indeed, given that the transplant experiment involving forma *incrustans* was halted prematurely by a freshwater intrusion, these experiments need to be repeated and allowed to run for a longer time. However, it is also possible that forma *incrustans* is a distinct, cryptic species that is incapable of branch production. We are currently exploring this possibility through analysis of DNA sequences from each of the morphotypes.

Hill (1999) suggested that the spicule- and spongin-rich cortex found in forma *incrustans* and forma *rigida* is an antipredator defense. He found that the tissue strength of forma *rigida* exceeded 10 N and forma *incrustans* was approximately equal to 5 N, whereas forma *variens* was near 2 N (Table 1). He also found that spongivores rapidly consumed the choanoderm of forma *rigida* when the cortex was removed. To assess the possibility that the cortex is an antipredator defense, we measured changes in spicule concentration as a proxy for tissue strength, given that there is a positive correlation between tissue stiffness and spicule concentration (Palumbi, 1986). We found that forma *variens* could increase spicule content in response to simulated predation events, and that forma *rigida* could reduce spicule content when protected from predation (Fig. 4). Although flow effects were not measured in the experiments involving

forma *rigida*, cages similar to these have been found to have no significant effect on flow (Hill, 1998). However, statements about the causes of the observed decreases in spicule density must be properly qualified. Nonetheless, skeletal plasticity appears to be a property of both forma *variens* and forma *rigida*. In future experiments, we are interested in determining whether spongin production also increases in areas of damage. The increase in spicule concentration observed in the artificial predation experiment may represent a generalized response to damage, but any damaged tissue would have to be repaired after a predatory attack, so the morphologic response we observed may serve an important antipredator function. This is clearly an area that requires additional experiments.

We propose that the large cortex in both forma *incrustans* and forma *rigida* represents an inducible defense. Four factors have been identified as prerequisites for the evolution of inducible defenses (Havel, 1987; Sih, 1987; Harvell, 1990; Tollrian and Harvell, 1999). First, inducing agents must have a temporally or spatially variable impact. Second, reliable cues concerning the inducer must be present so that a resistant morphology can be adopted. Third, induced defenses must be effective against inducers. Finally, it is hypothesized that inducible defenses must be costly, but costs are offset by fitness gains achieved in the defended state.

The *A. variens* system meets the first prerequisite since the reef has two discrete patches for predation risk: high-risk on the fore-reef, and low-risk in lagoonal habitats. Forma *variens* is located in an environment where predators are absent, whereas the other morphs exist in an environment where the selective pressure of inducers (*i.e.*, spongivores) is strong. Our artificial predation experiment demonstrated that mechanical stimulation could serve as a cue to increase spicule concentration (Fig. 4), thus meeting the second condition for the evolution of inducible defenses. Additional experiments are necessary to address the third and fourth prerequisites for the evolution of inducible defenses in *A. variens*. Forma *variens* appears to lack defenses against angelfish (Figs. 2 and 3), but we have evidence that forma *variens* increases spicule concentrations in response to simulated attacks (Fig. 4). Anecdotal evidence indicates that the cortex of forma *rigida* and forma *incrustans* protects the choanosome (Hill, 1999). Although the idea was not tested in this study, we suggest that the production of a thick cortex (Table 1) represents a physiological cost since less biomass can be devoted to feeding, storage, or reproduction (the cortex has no choanocytic chambers). Observed decreases in spicule concentrations in the caging experiment involving forma *rigida* support the hypothesis that maintenance of a spicule-dense cortex is costly (Fig. 4). *Anthosigmella variens* appears to be a model system in which to determine whether morphology can serve a defensive function, and whether that defense can be induced.

Although the importance of chemical defense in sponges should not be underestimated, there are several reasons to continue to look for evidence of morphological defense in sponges. First, 31% of Caribbean sponges that have been examined to date are chemically undefended (Pawlik *et al.*, 1995). Many of these sponges are abundant on reefs but are not common items in the diets of spongivores (Randall and Hartman, 1968). Furthermore, according to Randall and Hartman's (1968) rankings, five of the top seven sponges most commonly eaten by fish belong to the category designated as unpalatable by Pawlik *et al.* (1995), indicating that the defenses Pawlik and colleagues identified are not very effective against spongivores. Anecdotal evidence also indicates that skeletal structures may protect sponges from predation. During one dive, we observed more than five angelfish (gray, french, and blue) rapidly consuming the interior portions of a damaged *Geodia neptuni* sponge (the sponge appeared to have been bitten by a Hawksbill turtle). It seems that *G. neptuni* is normally capable of fending off fish predators given that *Geodia* spp. were rarely encountered in the stomach contents of spongivorous fish (Randall and Hartman, 1968). It should be noted that although *Geodia* spp. apparently lack chemical defenses against fish (Pawlik *et al.*, 1995), they have an impressive cortex that might serve as a morphological defense. *Anthosigmella varians* may also use the cortex to protect itself from predators because when *A. varians* forma *rigida* and forma *incrustans* are cut open, angelfish rapidly consume the choanoderm (Hill, 1999).

There is common agreement that sponges face strong selective pressure from spongivores. Whether skeletal structures can serve as antipredator defenses remains an open question. The defensive function of the sponge skeleton deserves greater attention, and should be expanded to include the possibility of synergisms between structural and chemical defenses, as has been demonstrated by Hay *et al.* (1994) for seaweeds. In sponges, spicules may serve to abrade digestive surfaces, thus facilitating the intake of sponge-derived secondary compounds. In addition, spicules may increase handling time of food items, thus influencing optimal foraging behaviors of spongivores. Additional field experiments directed at identifying costs associated with the *A. varians* cortex, and determining the potential effectiveness of the cortex as an antipredator defense, are necessary. *A. varians* clearly provides a unique combination of traits to explore the adaptive significance of phenotypic variation, and may provide insights into general evolutionary responses on coral reefs.

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